the matrix were the cristae). One theme in Palade's paper was that these structural characteristics provided ample opportunity for the types of biochemical reactions identified in cell fractions. In contrast, Sjöstrand's interpretation (bottom right) yielded multiple pieces of inner membrane that sometimes touched the inner layer of the outer membrane but were structurally separate – they were discontinuous both with the outer membrane and with each other. In the type of cell Sjöstrand used for his earliest micrographs, exhibiting plate-shaped rather than puzzle-piece-shaped inner membranes in 3D, the inner membranes typically extended across the entire 2D section, touching at both ends – the "complete septa" referred to by Palade. Regardless of how completely the mitochondria were partitioned in Sjöstrand's account, the resulting topography would turn out to be inconsistent with an important biochemical account proposed in 1962 and eventually accepted (Mitchell's chemiosmotic hypothesis; see Figure 6.8).

Sjöstrand never capitulated, but the intense conflict soon abated as Palade's interpretation gained ascendancy (for details, see Rasmussen, 1997[19]). Just a few years later Bourne (1962) could write matter-of-factly, "after a little controversy, it was agreed that the inner of these two membranes was extended into the interior of the mitochondria, in some cases touching or almost touching the other side" (p. 59).

Biochemists Further Fractionate Mitochondria

The cristae offered a plausible locus for the biochemical mechanism of oxidative phosphorylation, which biochemists already recognized as membrane bound. But exactly how were the enzymes recognized as responsible for the different reactions bound in the membrane? As Rasmussen emphasized, one of the features of the Rockefeller approach was that it promoted a collaborative inquiry with biochemists in which techniques for studying mitochondria were complementary, not competitive: Biochemical reactions could be localized in particular parts of the cell via chemical analysis of fractions while

[19] In discussing the interaction between Palade and Sjöstrand at the Third International Conference on Electron Microscopy in London, England, in July 1954, Rasmussen focused on the different uses to which each put his micrographs. Sjöstrand stressed using micrographs to make quantitatively precise estimates of membrane sizes. Palade, on the other hand, emphasized the importance of drawing out the connections with findings from other techniques such cell fractionation. Thus, Rasmussen commented, "Sjöstrand wanted to interpret his micrographs purely visually, judging fixation by the criterion of orderliness and seeking greater knowledge of molecular structure through ever-better resolution, whereas Palade, who was involved in cell fractionation himself, wanted to test micrograph interpretations against experiments on fractions" (1997, p. 139).